PALEOBOTANY.—New occurrences of the fossil quillworts called Isoetites. Roland W. Brown, U. S. Geological Survey.

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Except botanists, few people are familiar with the quillworts (*Isoetes*). As their common name implies, the quillworts have slender, pointed, although not stiff leaves that arise in a close spiral from a short stem or corm. In appearance they look somewhat like tufts of grass or sedge and may readily be mistaken for them. They are chiefly aquatic, growing along the muddy shores of quiet ponds in nearly all parts of the world.

On the inside of the base of the leaf, which is in reality a sporophyll, is the sunken sporangial area that on the outer or earlier leaves bears megaspores and on the inner or later leaves, microspores. Thus, Isoetes is not a fern but is commonly called a fern ally. For further anatomical details the reader is referred to my first paper on fossil quillworts (Brown, 1939), in which I reviewed the distinguishing features of Isoetes as an introduction to the description of some fossils whose identity with the quillworts was for a long time unsuspected. In that paper I defined two species, Isoetites serratus Brown from the Cretaceous, and I. horridus (Dawson) Brown from the Tertiary. Since then, as a result of field work and a closer inspection of the collections of fossil plants in the U.S. National Museum, new localities extending the range of Isoetites have been found and some new morphological information has appeared. In one instance the range of recognizable isoetalean remains is greatly extended backward in time.

Not long ago, speculating about the ancestral lineage of the Paleocene Isoetites horridus, I was reminded of the illustrations of some curious specimens described as Lepacyclotes [properly, Lepidocyclotes] by Ebenezer Emmons (1856, p. 332, pl. 3, figs. 4, 6) from the Deep River Triassic coal field southwest of Raleigh, N. C., the most recent discussion of which is by Reinemund (1955). Emmons's collection of plants from this area, long thought to be lost (Ward, 1900, p. 274–277; Fontaine, 1900, p. 277–279),

was found at Williams College, Williamstown, Mass., and transferred to the U. S. National Museum. Examining Emmons's specimens intently, I presently found features in them that are clearly identical with those on the previously described species of *Isoetites*. Lepacyclotes is therefore renamed as

Isoetites circularis (Emmons) Brown, n. comb. Figs. 5, 8, 9, 11, 13

Lepacyclotes circularis Emmons, Geol. rept. midland counties, N. C. p. 332, pl. 3, fig. 4. 1856; American geology, pt. 6, p. 130, pl. 3, fig. 4. 1857.

Fontaine, U. S. Geol. Survey Mon. 6, p. 119, pl. 49, fig. 8 [called *Araucarites carolinensis* Fontaine in plate legend], 1883; U. S. Geol. Survey 20th Ann. Rept., pt. 2, p. 311, pl. 47, fig. 4. 1900.

Daugherty, Carnegie Inst. Washington Publ. 526, p. 81, pl. 15, figs. 1, 2, 1941.

Lepacyclotes ellipticus Emmons, Geol. rept. midland counties, N. C. p. 332, pl. 3, fig. 6. 1856; American geology, pt. 6, p. 129, pl. 3, fig. 6. 1857

Fontaine, U. S. Geol. Survey Mon. 6, p. 118, pl. 52, figs. 4, 4a [called Araucarites carolinensis Fontaine in plate legend]. 1883; U. S. Geol. Survey 20th Ann. Rept., pt. 2, p. 311, pl. 47, fig. 5; pl. 48, 1900.

Emmons characterized Lepacyclotes as follows: "Disk circular or elliptic and formed of numerous scales arranged in a circle or in that of an ellipse; scales terminating outwardly in triangular points, which form a border outside of a circular ridge". Describing the two species, circularis and ellipticus, he added several details: "Scales with a ridge upon the back, bounded by two shallow furrows or depressions. Sometimes furnished with a stem which traverses the disk in the direction of its long diameter. . . . At first, it appeared to me that it was an accidental accompaniment; but having seen it already, three or four times, and always lying in this direction, I believe it should be regarded as a stem, or support of the disk, and that it is part of the plant". He dismissed the idea that Lepacyclotes might represent a cycad or conifer and regarded the plant as something unknown to him.

Fontaine's first guess was: "This plant is evidently a cone of a conifer near to Araucaria." Later he noted a significant fact: "The epidermal tissue of the scales, which is in many cases preserved, is exactly like that of Equisetum rogersi..." The word "exactly" here is perhaps too strong; but "much" or "very" would be appropriate. Fontaine's second guess, therefore, was that the specimens represent parts of a horsetail strobilus.

Daugherty identified his material from the Chinle formation (Triassic) in the Petrified Forest National Monument near Holbrook, Arizona, with that described by Emmons, and concluded that it represents "the basal portion of the flower of a Williamsonia," that is, a kind of cycadeoid. As I have not had an opportunity to examine Daugherty's specimens I enter his citation in the foregoing synonymy with a little hesitation.

From the evidence about to be submitted it can be concluded that *Isoetites circularis* is not an araucarian cone, a cycadeoid flower, or a horsetail strobilus, but that it represents a quillwort.

Spores. In Fig. 13, magnified three times, the large, round, tetrahedral megaspores can be seen matted together as black incrustations. Maceration of this material with nitric acid and potassium chlorate was not very successful. Nevertheless, with a binocular microscope, the spores and their triradiate ridges can be seen clearly, but other markings are obscure. In Fig. 8, natural size, of another specimen, faint, rounded cavities on both sides of the central ridge indicate the impressions of spores. In none of this Triassic material, however, have I found a specimen that definitely shows microspores, but such specimens should be looked for. The tetrahedral megaspore, it should be remarked, is general in the fern allies.

Sporangia. As in living Isoetes, the sporangium in the Triassic specimens was at the base of the leaf (sporophyll) on the ventral (inner) side. This part of the leaf seems to have been a more or less distinct segment, for the fossil sporangia are often found separately without traces of the sterile leaf parts but with a fairly sharp line showing where the rest of the leaf was originally attached. The sporangia are somewhat squarish (Figs. 5, 13) but in some instances narrowed rapidly to the point of attachment (Figs. 8, 11). Above the sporangium

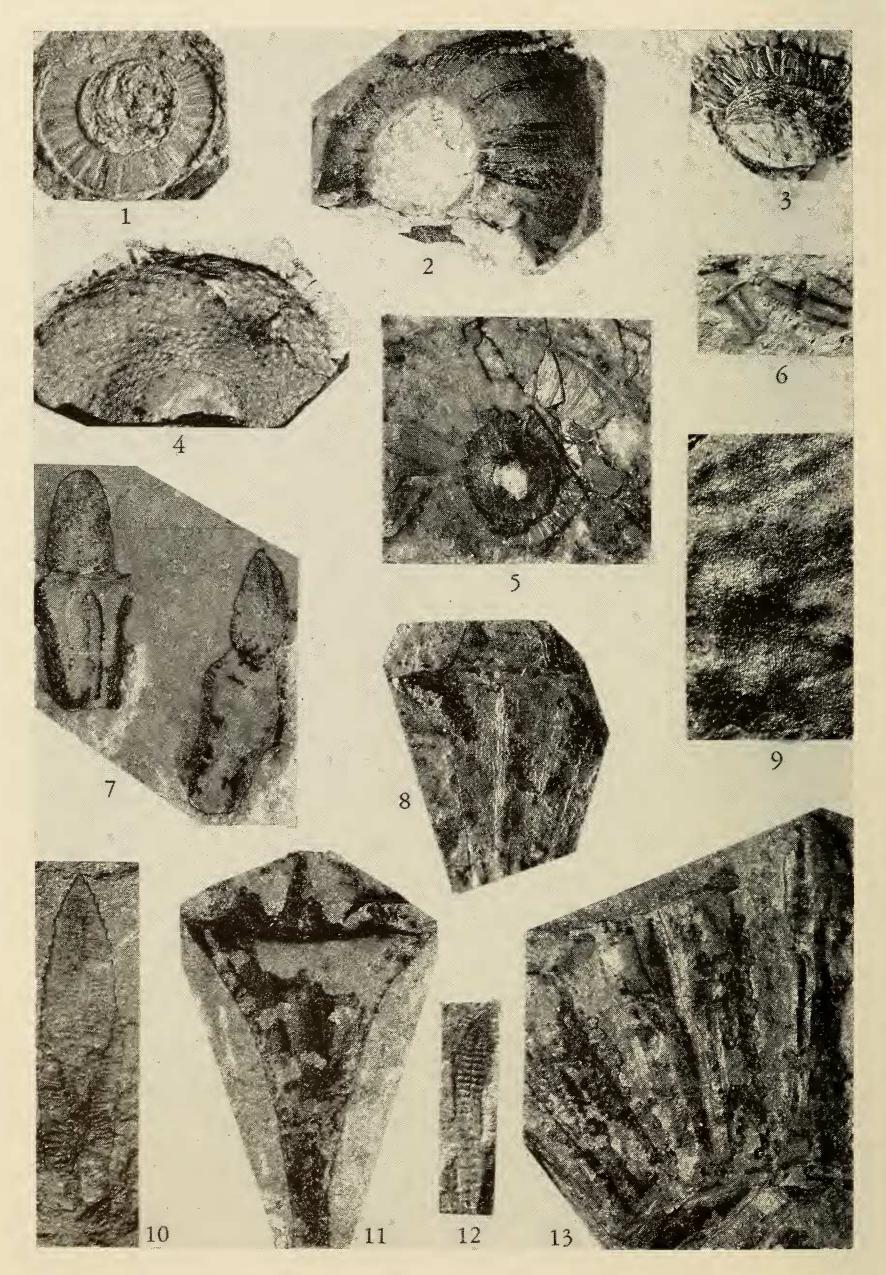
was a persistent triangular ligule (Fig. 11) somewhat larger than but similar to those on specimens (Fig. 3) from the Hanna formation (Eocene), northeast of Hanna, Wyo. Behind and beyond this, distally, the sterile part of the leaf continued for an indefinite distance to its tip, the nature of which is unknown in these specimens. No remains of the sterile parts of the leaves have been seen, except short fragments that sometimes are present at the sides of the ligules. Perhaps this part of the leaf, as suggested before, was easily detached and lost, or perhaps the collections from the Carolina area were not made with an eye for such material. Consequently, it is not known whether or not these leaves resembled those of the toothed Cretaceous I. serratus (Figs. 10, 12, and Brown, 1939, fig. 5) and the entire or sparsely toothed Tertiary I. horridus (Brown, 1939, fig. 6). They should be searched for in future collecting.

These sporangia are in general larger than those of the Cretaceous, Paleocene, and Eocene species (Figs. 1, 3, 6, 7) but are arranged in a close spiral (Fig. 5, similar to the Paleocene specimen, Fig. 4) around a so-called corm or stem that is not noticeably lobed as it often is in living species.

Surface features. Magnified 15 times, the surface of *I. circularis* is a fine pattern of minute rectangular papillations quite similar to that observed on the Cretaceous and Tertiary species (Brown, 1939, fig. 4). It also resembles closely the surface of *Equisetum*, another fern ally.

Other occurrences. Besides the occurrences of *Isoetites* already referred to or cited in the legend to the figures, two others, not here illustrated, need to be reported. One is a corm with a circlet of sporangia similar to those shown in Figs. 1 and 5. It was collected by H. R. Bergquist, of the U.S. Geological Survey, in 1946, from basal Upper Cretaceous ferruginous sandstone (Lewisville member of the Woodbine formation), 5 miles southeast of Dexter, Texas. The second consists of characteristic megaspores obtained by Duncan Heron, Department of Geology, Duke University, by washing samples from outcrops of the Tuscaloosa formation (Upper Cretaceous) in North and South Carolina in 1957. These specimens are at that university.

Concerning the habit and ecology of *Isoctites* little is known, but a bit can be conjectured. Because the fossils are nearly always associated with *Equisetum* the inference that the living



Figs. 1-12.—(See opposite page for legend).

plants were adapted to moist conditions seems reasonable. The Cretaceous and Tertiary species are frequently found with remains of aquatic plants called *Trapa?*, whose foliage has all the appearance of having been a floating rosette. The peculiar squarish features seen along the midline on leaves of *Isoetites* are the outward expression of collapsed inner air spaces, and this, coupled with the fact that the ends of the leaves were flat and spatulate suggests that the leaves were adapted to resting on a water surface, as they are in some living species of *Isoetes*.

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Fig. 1.—Isoetites horridus (Dawson) Brown, showing a circle of sporangia, with megaspores and microspores, around the corm. U.S.G.S. loc. 5144, in Tin Pan Canyon, northwest of Raton, N. Mex. Raton formation (Paleocene). Fig. 2.—I. serratus Brown, Loc. 9332, northeast of Rock Springs, Wyo. Mesaverde formation (Upper Cretaceous). Fig. 3.—I. horridus, showing small, pointed ligules above the sporangia. Loc. 8548 northwest of Hanna, Wyo. Hanna formation (Eocene). Fig. 4.—I. horridus, southeast of Rock Springs, Wyo. Fort Union formation (Paleocene). Figs. 5, 8, 9, 11, 13.—I. circularis (Emmons) Brown, n. comb., showing (5) a corm surrounded by sporangia, (8, natural size, 11, ×3), single sporangia with ligules and fragments of the sterile parts of leaves, (9, ×15) the papillated surface pattern, (13, ×3) part of a corm with sporangia on whose surface can be seen patches of a black incrustation consisting of matted, roundish, tetrahedral megaspores. Deep River coal field, southwest of Raleigh, N. C. Pekin formation (Upper Triassic). Fig. 6.—I. horridus, showing sporangia with fragments of the sterile parts of the leaves and their undulate margins. Loc. 8881, one-half mile northwest of Ramah, Colo. Dawson arkose (Paleocene). Figs. 7, 10.—I. serratus, showing (7, ×3) sporangia and fragments of the sterile parts of the leaves, (10, ×3) the spatulate, serrate tip of a leaf. Loc. 9384, north side of Cortez, Colo. Dakota sandstone (Upper Cretaceous). Fig. 12.—I. serratus, ×3, showing spatulate tip of a leaf and undulations along the midline that represent collapsed inner air spaces. Loc. 4806, northeast of Rock Springs. Mesaverde formation (Upper Cretaceous).

All figures are natural size except as noted, and all specimens are in the U.S. National Museum.